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Studies on the growth of root hairs in solutions
VII. Further investigations on collards in calcium hydroxide

CLIFFORD H. FARR

(WITH FOUR TEXT FIGURES)

The preceding papers of this series[1] presented the results of researches performed during 1925 and 1926 upon the rate of elongation of root hairs, and to a less extent of roots, as well as upon structural features associated with the development of roots and root hairs of the variety of *Brassica oleracea* known as Georgia collards, while immersed from 12 to 16 hours in flowing solutions of calcium chloride of various hydrogen-ion and molar concentrations. There was also included a preliminary study of solutions of calcium hydroxide and calcium nitrate. The present paper presents further investigations with calcium hydroxide done during 1927, and includes not only the growth rate of root hairs, but also of the root itself, and data as to the development of roots in these solutions.

The technique employed in this study was very nearly the same as used in the research reported in the preceding papers—namely, germinating the seed upon filter paper, and transferring the seedlings, when the radicles are approximately 1 cm. long, to a chamber on the stage of the horizontal microscope, through which the solution flows at a constant rate for a period of several hours. Measurements of root elongation and of other aspects of

[1] Farr, C. H. Studies on the growth of root hairs in solutions.

I. The problem, previous work, and procedure. Amer. Jour. Bot. **14**: 446–456. *f. 1.* 1927.

II. The effects of concentrations of calcium nitrate. Amer. Jour. Bot. **14**: 497–515. *f. 2.* 1927.

III. The effects of concentrations of $CaCl_2$ and $Ca(OH)_2$. Amer. Jour. Bot. **14**: 553–564. *f. 3, 4.* 1927.

IV. The pH-molar-rate relation for collards in calcium chloride. Amer. Jour. Bot. **15**: 6–31. *f. 5–10.* 1928.

V. The root hair as an index of root development. Amer. Jour. Bot. **15**: 103–113. *f. 11–15.* 1928.

VI. Structural responses to toxic pH and molar concentrations of calcium chloride. Amer. Jour. Bot. **15**: 171–178. *pl. 7–9.* 1928.

[The BULLETIN for April (**55**: 181–222) was issued June 14 1928.]

root development were made after 12 hours immersion in the solution; and data were collected on the rate of root hair elongation for the interval of 13 to 16 hours after immersion.

However, certain alterations in the technique were effected, which were conducive to greater accuracy and convenience in prosecuting the study. One of these consisted in the use throughout of buffer solutions as standards for hydrogen-ion determinations in place of the color chart published in Clark's book (142). To the indicators previously used there were added Brom Cresol Green and two new indicators, Nitro Yellow, pH 10.0 to 11.6, and Sulpho Orange, pH 11.0 to 12.6. The buffer solutions containing the indicators were arranged in test tubes held by racks about the margin of an octagonal revolving platform, in order to secure equal illumination and give greater facility and rapidity to the making of determinations. In this study three hydrogen-ion determinations were made for each set of apparatus in each experiment.

The apparatus was modified slightly. Pyrex glass tubing and stopcocks and separatory funnels were used as well as the Pyrex flasks formerly employed. The best pure gum black rubber tubing was used, after boiling it in caustic alkali as before. A minor modification consisted in the use of a filter pump instead of the aspirator bottles, thus allowing greater ease of manipulation and a longer period, as well as a more rapid rate of aeration.

More extensive data were obtained as to root development. On the other hand, readings on root hair elongation were not made quite so frequently. Instead of the ten-minute interval previously employed, it was found possible to follow the root hairs individually by observing them every twenty or thirty minutes. This gave greater freedom to the observer, and resulted in no reduction in precision. As noted before, the first and last readings are the most significant ones. The object of taking readings within the three hour period is to preserve the identity of the root hairs, and to ascertain whether or not they stop growing during the interval. Whether the rate is constant or not is shown nearly as well by 20- or 30-minute readings as by 10-. In the tables of data given below, however, the increments are prorated on a ten-minute interval basis, in order that equivalent units of time may be represented.

In order to secure more data, it seemed advisable to measure a few hairs which did not lie within the scope of the micrometer scale, which was movable longitudinally, but not laterally. Since errors might occur if the chamber were moved for the purpose of making these measurements accurately every 20 to 30 minutes, it was decided to accurately measure these hairs at the beginning and at the close of the three-hour period, and to approximate their length by optical projection of the lines of the scale for the intermediate readings. For this reason no significance should be attached to an apparently sudden change in the growth rate of the first or the last root hairs in any one of the series of data given below. This is simply a correction of an error in making the earlier readings.

The rate of elongation of root hairs in calcium hydroxide is of general physiological significance, because it involves an exceedingly simple solution containing theoretically only two ions, Ca and OH, and because it is a very simple process, involving perhaps only cell wall deposition and water absorption. It is of special importance in connection with a study of root hair elongation in single calcium salt solutions, as it forms a very essential part of the three-dimensional graphs. It therefore seemed advisable that the study made in 1926 (III) be confirmed or corrected. In so doing it was decided to use more frequent pH intervals, in order that the curve might be more accurately plotted. (See table 19).

A comparison of the above results with those obtained in a similar study the preceding year and already published (III) will be of interest. This is given in table 20, in which the averages for 1927 are computed, as for 1926, on the entire number of hairs measured in each solution, without reference to the side of the root upon which they occured. The results, however, would not have been fundamentally different, if they had been calculated separately for the two sides of the roots respectively.

The data given table 20 are presented graphically in figure 16a. It will be noted that the four curves—namely the average and maximum for 1926 and 1927, respectively—are consistent in all essential features. The marked elevation of the maximum graph for 1927 at pH 10, it will be observed, is due to a single root hair, which grew at the rate of 114.1 microns per hour, which is 4.3 microns faster than any root hair so far

TABLE 19

Root hair elongation of collards in calcium hydroxide.[a]

pH	INCREMENTS IN MICRONS PER TEN-MINUTE INTERVAL	MICRONS PER HOUR		
		Av.	Max.	Mean
7.0	14 hairs, no growth	0	0	0
7.5*f*[b]	9–12–12– 7– 7–10–10–10–12–12–10–10– 7– 7–11–11–11–11	56.0		
	12–12–12– 8– 8–11–11–11–15–15–11–11– 7– 7–13–13–12–12	62.8		
	16–16–12–12–12–12–12–12–12–12– 9– 9– 7– 7–13–13–10–10	61.5		
	12–16–16–10–10–12–12–12–12–12–10–10– 3– 3–12–12–10–10	60.6		
	13–12–12– 8– 8–12–12–12– 9– 9– 8– 8– 9– 9–12–12– 5– 5	53.8		
	13–12–12– 6– 6– 5– 5– 5– 2– 2–15–15– 7– 7–17–17–12–12	53.8		
	12–14–14– 7– 7–10–10–10– 5– 5– 6– 6– 2– 2–11–11– 6– 6	44.8		
			62.8	56.2
7.5*f*[b]	18–14–14–10–10– 9– 9– 9– 8– 8– 6– 6– 3– 3– 1– 1– 5– 5	49.8		
	15–15–15–10–10– 8– 8– 8– 5– 5–10–10– 7– 7– 1– 1– 4– 4	45.1		
	14–12–12–10–10– 4– 4– 4–19–19– 0– 0– 0– 0–12–12–12–12	49.5		
	22–14–14–12–12–10–10–10–10–10– 5– 5–10–10–10–10– 4– 4	52.9		
			52.9	49.3
8.0*f*	10–10– 8– 8–10–10– 5– 5–10–10– 8– 8–13–13– 8– 8–12–12	47.6		
	12–12–12–12–14–14– 8– 8–11–11– 9– 9–12–12–10–10–10–10	53.5		
	10–10– 8– 8–14–14– 9– 9–10–10– 7– 7–11–11– 3– 3– 7– 7	45.1		
			53.5	48.7
8.0*t*	15–15–12–12– 9– 9–12–12– 8– 8–13–13–15–15–10–10–10–10	59.1		
	12–12–13–13–11–11–12–12– 9– 9–13–13–12–12– 9– 9–12–12	59.4		
	13–13–15–15– 6– 6–12–12–12–12–13–13–19–19–11–11–14–14	70.2		
	13–13–15–15– 7– 7–16–16–11–11–14–14–14–14– 9– 9–13–13	67.1		
	20–20–15–15– 7– 7–16–15– 8– 8–14–14–19–19–12–12–13–13	69.9		
	13–13–13–13–12–12–12–12– 8– 8–6– 6–12–12–12–12– 13–13	59.7		
	11–11–17–17–17–17–13–13–11–11–15–15–17–17–13–13–13–13	80.1		
			80.1	66.5
8.5*f*	11–11–10–18–19–19–12–11–12–15–15–15–12–12–12– 8– 8– 8	70.5		
	9–10– 9– 10– 9–10– 3– 3– 4– 0– 0– 0– 1– 1– 1– 0– 0– 0	21.9		
	9– 9– 9–12–13–12– 7– 7– 8– 5– 4– 5– 4– 4– 4– 0– 0– 0	34.9		
	12–11–12–13–13–12– 5– 4– 5– 7– 7– 7– 8– 9– 8– 0– 0– 0	39.8		
	6– 7– 6– 7– 7– 7– 0– 0– 0– 0– 0– 0– 1– 1– 1– 0– 0– 0	13.4		
	11–11–11–16–15–16–12–13–12–12–13–12–13–12–13–11–10–11	69.6		
			70.5	41.7
8.5*t*	8– 7– 8– 6– 5– 6– 7– 6– 7– 1– 1– 1– 0– 0– 0– 0– 0– 0	19.7		
	9– 9– 9– 6– 5– 6– 8– 7– 8– 3– 4– 3– 0– 0– 0– 0– 0– 0	23.7		
	8– 7– 8– 5– 6– 5– 8– 8– 8– 3– 4– 3– 0– 0– 0– 0– 0– 0	22.8		
	8– 8– 8– 8– 7– 8– 7– 6– 7– 1– 2– 1– 0– 0– 0– 0– 0– 0	22.2		
	8– 9– 8– 8– 7– 8– 6– 6– 6– 0– 0– 0– 0– 0– 0– 1– 0– 1	18.8		
	7– 7– 7– 6– 7– 6– 6– 5– 6– 3– 2– 3– 0– 0– 0– 0– 0– 0	20.0		
			23.7	21.2
9.5*f*	13–12– 6– 5– 6– 7– 6– 7– 7– 7– 7– 9– 9– 9– 4– 4– 4– 4	45.1		
	5– 5– 8– 7– 8– 8– 8– 8– 9– 8– 9– 8– 8– 8– 9–10 9– 9	43.6		
	10–11–12–13–12–12–11–12–14–15–14–13–14– 3–10–10–10–10	66.2		
	9– 9–11–12–11–11–11–11–13–14–13–13–14–13–11–10–11–11	64.6		
	14–13– 9–10–19–11–11–11–10– 9–10–14–13–14–10–11–10–11	62.6		
	5– 5– 5– 5– 5– 6– 5– 6– 5– 5– 5– 8– 6– 8– 6– 7– 6– 7	33.0		
	0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0– 0	0		
			66.2	45.0

TABLE 19—(cont.)

pH	INCREMENTS IN MICRONS PER TEN-MINUTE INTERVAL	MICRONS PER HOUR		
		Av.	Max.	Mean
9.5*t*	7- 7- 8. 7- 7- 7- 8- 7- 6- 5- 6- 3- 4- 3- 4- 5- 4- 5	32.1		
	8- 8- 1- 0- 1- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0	5.7		
	8- 9- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0	5.7		
	12-12- 1- 1- 1- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0	10.7		
			32.1	13.6
10.0*f*	15-15-15-13-12-13-12-11-12-26-25-26-16-17-16-16-16-23	92.5		
	14-14-14-14-12-13-12-11-12-11-24-25-24-17-18-17-18-13	84.8		
	18-18-18-18-16-15-16-17-17-17-28-27-28-15-15-15-15-38	108.7		
	14-14-14-14- 9-10- 9-12-13-12-25-24-24-14-15-14-15-19	84.2		
	18-19-18-18-15-15-15-19-19-19-30-30-30-19-19-19-19-27	114.2		
			114.2	96.9
10.0*t*	13-14-13-13-15-16-16-18-17-18-14-13-13-12-13-12-13-23	82.6		
	12-11-12-12-13-14-13-19-18-19-11-12-11-15-15-15-15-13	74.6		
	10-11-10-11-15-15-15-13-12-13-10-11-10-13-14-13-14-13	76.1		
	13-14-13-14-15-16-15-18-18-18-11-11-11-14-15-14-13-14	79.5		
	12-11-12-12-16-15-16-17-18-18-12-13-12-12-13-12-13-13	76.7		
	13-14-13-13-15-15-16-15-15-16-11-11-11-13-14-13-14-10	75.2		
			82.6	77.4
11.0*f*	8- 9- 8-13-14-13- 8- 9- 8-12-11-12-10-10-10-13-14-13	57.5		
	8- 8- 8- 6- 5- 6- 8- 7- 8-10-10-10- 3- 4- 3-13-14-13	44.8		
	7- 8- 8- 3- 4- 3- 4- 5- 3- 6- 5- 6- 0- 0- 0- 1- 1- 1	20.3		
	9- 9- 9- 8- 9- 8- 8- 9- 8- 9- 9- 9- 7- 7- 7- 6- 5- 6	47.3		
	5- 5- 5-11-11-11- 7- 7- 7-12-12-12- 8- 8- 8-10-10-11	52.9		
	8- 9- 8- 6- 6- 6- 4- 3- 3-11-12-11- 5- 4- 5-10- 9-10	41.4		
			57.5	44.0
11.0*t*	7- 8- 7- 5- 6- 5- 1- 2- 1- 5- 6- 5- 1- 2- 1- 3- 2- 3	21.9		
	6- 7- 6- 7- 7- 7- 2- 3- 2- 8- 8- 8- 4- 5- 4- 4- 5- 4	30.2		
	7- 6- 7- 5- 6- 5- 1- 2- 1- 4- 5- 4- 2- 3- 2- 0- 0- 0	18.8		
	2- 3- 2- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0	2.3		
			30.2	18.3
11.5*f*	0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 5- 5- 5	4.8		
	0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 4- 4- 4	3.9		
	0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 8- 7- 8	7.3		
	4 hairs, no growth	0		
			7.3	2.7
11.5*t*	2- 1- 2- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 3- 4- 3	4.8		
	3- 4- 3- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0- 0	3.3		
	1- 0- 1- 0- 0- 0- 0- 0- 2- 3- 2- 1- 2- 3- 7- 6- 7	11.0		
	3- 4- 3- 0- 0- 0- 0- 0- 0- 0- 0- 4- 5- 4- 7- 8- 7	14.1		
			14.1	8.3

[a] The average values in microns per hour are based on the first and last readings and represent the significant data; the individual values are only approximate. See explanation in text.

[b] *f* refers to the side away from which the solution is flowing; *t* refers to the side of the root toward which it is flowing.

measured. This is apparently a somewhat abnormal case; but it serves to confirm the conclusion previously reached (III) as to the greater effectiveness of hydroxide than of chloride or nitrate in supporting root hair elongation. It is to be noted that the averages for 1926 and 1927 at pH 10 are almost identical. The other marked difference between the curves for the two years is in the low level to which the graphs for the latter year drop at pH 8.5 and 9.5. This it will be observed, is due to the cessation of growth in a number of hairs during the three

TABLE 20

Summary of root hair elongation in calcium hydroxide

pH	1926		1927		COMPOSITE	
	Maximum	Average	Maximum	Average	Maximum	Average
7.0	0	0	0	0	0	0
7.5			62.8	53.7	62.8	53.7
8.0	78.7	65.8	80.1	61.2	80.1	63.5
8.5	62.2	47.8	70.5	31.4	70.5	39.6
9.0	55.0	45.2			55.0	45.2
9.5			66.2	33.6	66.2	33.6
10.0	85.4	85.1	114.1	86.3	114.1	85.7
10.5						
11.0	51.0	41.1	57.5	33.7	57.5	37.4
11.5			14.1	4.5	14.1	4.5
12.0	6.2	5.1			6.2	5.1

hour period. Had measurements of these hairs been begun a little earlier, this departure would doubtless not have occurred.

In the last two columns in table 20 there is given a combination of the data for the two years. In the one column is given the greater of the two maxima in cases where the same hydrogen-ion concentration was studied both years; in the other column is given an average of the two averages in these cases. It is apparent that the maximum composite curve is the smoother and more consistent. A theoretical pH curve for elongation of root hairs of collards in calcium hydroxide is given in figure 16b.

Before proceeding to a consideration of the correlation of the rate of root hair elongation with the rate of elongation and other features of the development of the root, it may be well to consider in what extent other factors, besides hydrogen-ion

concentration, may have been potent in determining the rate of elongation of root hairs. The author has already (II) discussed the factors involved in the variation of successive readings of individual root hairs. It was concluded that the difficulty in taking readings to a precision of less than several microns, and the pulsations in the elongation of the hair were of prime importance in this connection. In the same place the author has also discussed the variations in the rate of elongation

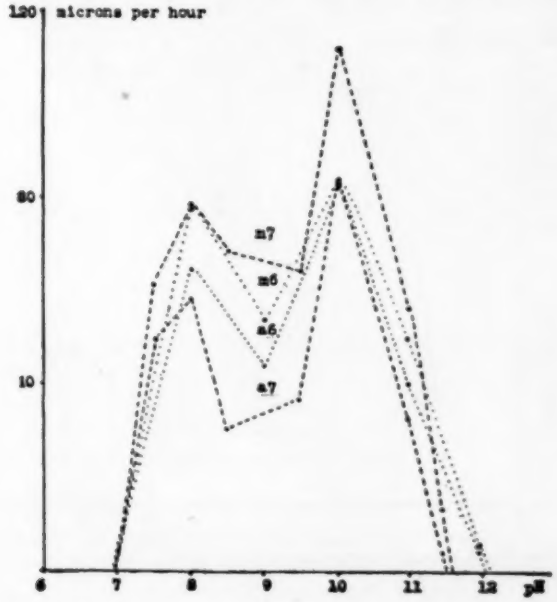

Fig. 16a. Root hair elongation in calcium hydroxide, actual.
m7: maximum rate as obtained by experiments in 1927.
a7: average rate as obtained by experiments in 1927.
m6: maximum rate as obtained by experiments in 1926.
a6: average rate as obtained by experiments in 1926.

of the different root hairs in the same solution. This was attributed largely to deviations of the root hair from a plane exactly at right angles to the direction of observation. Another factor involved in this variation is also brought out in the data given in table 19—namely, the difference between the rates of elongation of hairs on the two sides of the root. It is also to be noted that in some solutions the hairs cease to grow when they

have attained a certain maximum length for that solution. This seems to be the case with solutions of calcium hydroxide of pH 8.5 and 9.5, on the side of the root toward the solution. Obviously the root hairs which are longer at the beginning of the three hour period will attain this maximum length first in most cases. In the tables of data, like table 19, the order of length of root hairs is from the distal to the proximal portion of the root; that is, the root hairs near the end of each series are usually longer than those near the first.

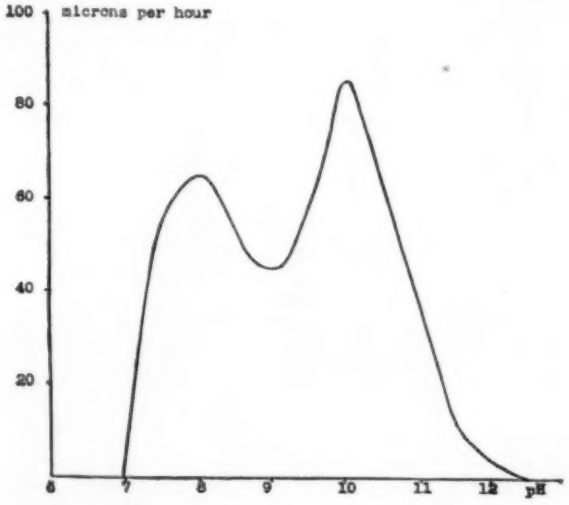

Fig. 16b. Root hair elongation in calcium hydroxide, idealized.

The three most important conditions which operated during these experiments, and which should be considered in connection with the data given above are temperature, rate of flow of the solution, and its hydrogen-ion concentration. It was not found possible to hold these absolutely constant during the experiment; but records of them were kept and are presented in table 21, which also includes a summary of the results obtained on root hair growth, presented in detail in table 19.

The rate of flow of the solution is given in drops per minute, determinations being made at the time of taking the temperature, and designated as R_1, R_2, and R_3, respectively. The date given in the table is that upon which the seedlings were inserted

into the apparatus in each case, and preceding that upon which the readings of growth rate were taken.

There seem to be no English words now in good usage for designating the side of the root toward which a solution is flowing, and the side away from which it is flowing. The terms *incoming* and *outgoing* involve the concept of absorption, which does not necessarily obtain. *Upstream* and *downstream* are not

TABLE 21

Conditions and summary of experiments with $Ca(OH)_2$

DATE	T_1	T_2	T_3	pH_1	pH_2	pH_3	R_1	R_2	R_3	MAXIMUM		AVERAGE		MEAN	RATIO
										t	*f*	*t*	*f*		*t*:*f*
7/6	18.0	18.0		7.5		6.0	4	1	10	52.9	*62.8*	49.3	56.2	52.7	1:1.14
7/7	19.5	18.0	19	8.0		7.2	11	7	7	*80.1*	53.5	66.5	48.7	57.6	1:0.73
7/14	22.0	19.5	21	8.5	8.5	7.5	7	7	7	23.7	*70.5*	21.2	41.7	31.4	1:1.97
7/13	22.0	19.5	21	9.5	9.5	7.5	12	10	10	32.1	*66.2*	13.6	45.0	29.3	1:1.31
7/10	20.5	18.0	20	10.0	10.0	8.6	7	0	10	82.6	*114.2*	77.4	96.9	87.2	1:1.28
7/11	21.0	18.0	21	11.0		11.0	11	10	6	30.2	*57.5*	18.3	44.0	31.1	1:2.40
7/12	22.0	19.0	21	11.5	11.0	11.0	7	6	6	*14.1*	7.3	8.3	2.7	5.5	1:0.58
														Mean	1:1.49

The three room temperatures given in table 21 were taken at the following times respectively:

T_1: about 7:30 P.M. at time of insertion of seedlings.
T_2: about 6:30 A.M. at time of general observations.
T_3: about noon, at close of period of readings.

The hydrogen-ion determinations were made as follows:

pH_1: solution in flask prior to aeration, about noon.
pH_2: same solution at close of experiment, about noon.
pH_3: solution flowing from apparatus, during readings.

applicable here, inasmuch as the current flows up against the roots. In aerial relations, the terms *windward* and *leeward* are appropriate; and it is their counterparts for aquatic relations that are here needed. The German words *zufliessend* and *abfliessend* are *a propos* in that language. I have decided to employ the words *affluent*, as meaning flowing towards, and designated by *t* in the tables, and *effluent*, as meaning flowing away from, and designated by *f*.

It is to be observed that all five series of root hair readings given in table 21—namely, those for the maximum and the average rate on each of the two sides of the root, and the mean

of the two averages—show two optima, one at pH 10 and the other at pH 8, except on the effluent side, where the second optimum is at pH 7.5. The effluent side in the maximum series also shows a third maximum at pH 8.5. This indicates that the solution on the effluent side is not the same as that on the affluent side.

Evidently at least two factors operate to alter the chemical composition and hydrogen-ion concentration of the solution as it moves from the affluent to the effluent side: the absorption of calcium from this extrememly dilute solution by the root and the root hairs on the affluent side; and the liberation of carbon dioxide by that side. In addition it is not unlikely that other cations may be given off in exchange for the calcium. Whatever the explanation of the alteration, the result is a decided difference in most solutions in the rate of elongation of root hairs on the two sides. The mean ratio shows that the rate is on an average of about 150 per cent as great on the effluent as on the affluent side. Very little difference exists in the lowest concentration, pH 7.5, and it is doubtful if any significance should be placed upon the difference in the highest concentration, pH 11.5. Ignoring these two concentrations for the moment, then, it is shown by the italicized numbers in the maximum series, and by the corresponding values in the average series, that the growth is greater on the affluent side at low concentrations and greater on the effluent side in medium and high concentrations. It would appear, therefore, that there must be some injurious factor in the solution at medium and high concentrations of the compound, and that this injurious factor is more potent on the affluent than on the effluent side. The pH graph for root hair elongation (figure 16) indicates that this factor is not calcium. We are, therefore, led to the conclusion that it must be the hydroxyl ion which is present in higher concentration with increase of the basic compound, or decrease in hydrogen ions, if the other theory of alkalinity is adopted.

Just how the concentration of the solution may operate to give a differential effect on root hair production and elongation on different sides of the root may be better elucidated by reference to figure 17. This is a more or less diagrammatic representation of the relation of the current of solution to the root surface. In *a* the direction of the current with respect to the

longitudinal aspect of the root is given; and in *b* and *c* the relation of the current to the transverse aspect. It is likely that the maximum amount of irrigation of the root by the current

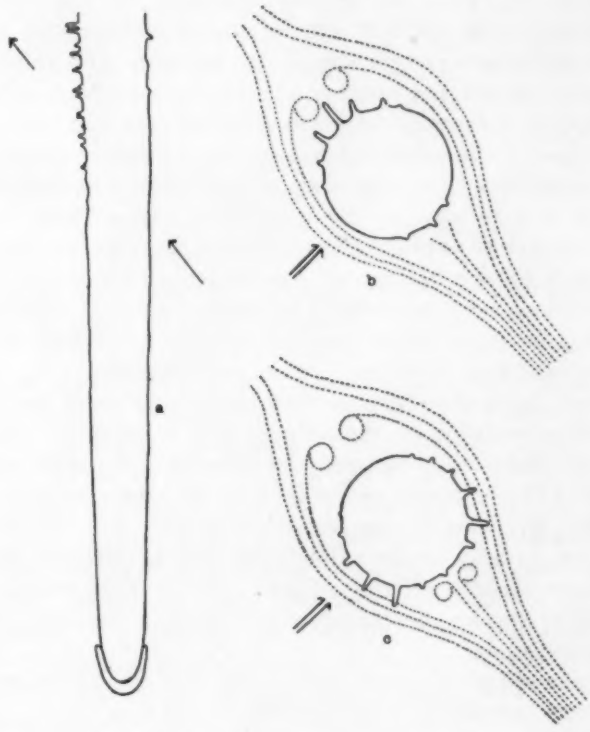

Fig. 17. Relation of direction of flow of solution to root hair production.

a. Longitudinal view of a root in a hypertonic solution (single arrows indicate direction of flow of solution).

b. Diagrammatic representation of transverse view of the region of root hair formation of a root in a hypertonic solution (double arrows indicate direction of observation through the microscope; broken lines represent paths of flow of solution in vicinity of root).

c. Diagrammatic representation of transverse view of the region of root hair formation of a root in a hypotonic solution (characters to be interpreted as in *b*).

takes place neither on the middle of the affluent side, nor on the middle of the effluent side, but rather on the lateral flanks slightly toward the affluent surface. On the optical horizon of

the affluent side the solution would remain quite stationary, or move in small eddies which would tend to circulate the same solution repeatedly against the root surface, with only a partial admixture of ions from the main stream. On the horizon of the effluent side there would be larger eddies, and hence a greater reduction in renewal of the solution. Therefore, in a solution in which the number of stimulating ions is below the optimum, a hypotonic solution, the poorest solution will be on the line of the effluent horizon. In a solution containing a slight overdose of nutrient ions, a hypertonic solution, the best solution will be also at the location of the effluent horizon. However, it does not follow that the best location in a hypotonic solution is on the horizon of the affluent side; nor is this the poorest place in a hypertonic solution. But, as is shown by figure 17, the affluent side is neither the best irrigated nor poorest irrigated in any solution, but is intermediate. We would, therefore, upon this basis expect the results upon the rate of root hair elongation on the affluent side to be more consistent and dependable than that on the effluent side for an accurate picture of the response of the root to the concentration of the solution. We should also expect that the root hairs would grow more rapidly on the effluent side in a hypertonic solution, and more rapidly on the affluent side in a hypotonic solution. All of these expectations are realized in the data given in the tables above.

An examination of the data given in table 21 reveals that there is no correlation between the rate of flow of the solution and the rate of elongation of root hairs. Somewhat more careful scrutiny is, however, necessary to convince one that there is no effect of temperature. It is to be noted that the matinal temperature, T_2, is relatively low, 18°C, for experiments in pH 7.5, 8.0, 10.0, and 11.0, all of which show a high rate of growth. The temperature was one degree higher for pH 11.5, and one and one-half degrees higher for pH 8.5 and 9.5, all three of which showed low rates. However, it is to be observed that the four solutions at 18°C. (matinal) gave average growth rates of 31.1, 52.7, 57.6, and 87.2, indicating little correlation with temperature.

Pearsall and Wray (196) have recently pointed out that the solubility of calcium soaps is exceedingly sensitive to

temperature variations. Inasmuch as, according to their interpretation, this is an important factor in the rate of cell wall formation, it might not be surprising to find a direct correlation between the rate of root hair elongation and the temperature of the solution which bathes the root hairs. Temperature could, however, hardly explain the marked differences shown in table 21. It is to be noted that the temperatures for the experiments with pH 10.0 and 11.0 were only 0.5°C. different in the evening, not different at all in the morning, and one degree different at noon, and yet the growth was only one-half as rapid in the latter solution.

Trelease and Trelease (197) have shown that for elongating 84 mm. the roots of wheat required 173 hours in 14°C., 102 hours in 19°C. and 80 hours in 30°C. This would mean a difference of about 3 hours per degree for the temperature range here represented, namely 18° to 22°, or a difference of about 3 per cent per degree. Cerighelli (192) found that the root length of peas is about twice as great at 20°C. as at 10°, and about two-thirds as great at 30° as at 20°. This would indicate that the effect of temperature upon root growth is at a minimum near 20°C. It seems, therefore, that the slight differences in temperature recorded for these respective experiments could not have altered the growth rate of the root hairs to any appreciable extent. This seems all the more likely in view of the duplication of the results obtained in 1926 by repeating the experiment a year later (figure 16).

This leaves hydrogen-ion concentration as the chief factor to which the variations in growth rate may be attributed. It is to be noted from table 21 that the determinations for the solution flowing from the exit tube (pH 3) are all from 0.5 to 2.0 pH units lower than the original solution in the flask, except in the case of pH 11.0, in which there was no change. Attention has already been called (IV) to the rise in the hydrogen-ion concentration of alkaline solutions as they pass through the chambers in which roots and root hairs are growing well. It is now to be noted that this drop in pH is apparently somewhat greater in solutions so dilute as those used here, when compared with the solutions upon which previous observations of the same type were made—namely, 0.008 and 0.020 M $CaCl_2$. This difference is very likely due to the absence of any buffer-

ing effect such as exists in the calcium cholride solutions to a limited extent. It should also be noted here that the solution as it flows from the flask is collected in an open test tube into which it flows at the rate of about ten drops a minute. The test for the solutions in the flasks, however, is made upon a sample taken directly from the flask and exposed to the air only a short time. It is therefore regarded as proper to consider the pH of the solution as it reaches the root hair as more nearly approaching that of the determination made upon the flask (pH_1 and pH_2) than the one made upon the overflow (pH_3).

TABLE 22

Root elongation and root hair length in $Ca(OH)_2$

pH	ROOT ELONGATION										MAXIMUM LENGTH OF ROOT HAIRS			
	1			2			3		Av.		1	2	3	Av.
	o	*l*	*d*	*o*	*l*	*d*	*o*	*l*	*d*					
7.5	3.0	4.5	1.5	5.0	9.0	4.0	8.5	10.5	2.0	2.5	250	450	300	333
8.0	5.0	13.5	8.5	4.5	6.5	2.0	3.0	6.0	3.0	4.5	400	350	550	433
8.5	5.0	10.5	5.5	7.5	15.0	7.5	7.5	12.0	4.5	5.8	500	500	600	533
9.5	6.0	10.5	4.5	5.0	10.5	5.5	8.5	15.0	6.5	5.5	250	500	600	450
10.0	1.5	7.5	6.0	4.5	9.0	4.5	3.0	7.5	4.5	5.0	800	400	500	566
11.0	4.0	6.0	2.0	5.0	7.5	2.5	15.0	18.0	3.0	2.5	200	200	400	266
11.5	3.0	7.5	4.5	4.5	6.0	1.5	3.0	7.5	4.5	3.5	150	100	0	83

The symbols used in this and the following tables are as follows:

o: original reading taken at time of insertion.

l: last reading taken 12 hours later.

d: difference between *o* and *l*, that is, the increment.

The readings for roots are given in millimeters; those for root hairs in microns.

We thus come to the conclusion that the effect of different concentrations of calcium hydroxide upon root hair elongation may be represented by a bimodal graph on the pH scale extending from pH 7.0 to pH 12.0 with two modes, the lesser optimum at pH 8.0 and the greater at pH 10.0. The reason for the depression between the two optima does not seem to be at present explicable on physico-chemical grounds. For reasons already given (IV) it does not seem attributable to an isoelectric point of the constituent proteins. There does, however, seem to be a very good basis for the difference in the elevation of the two optima. The one nearer neutrality is not so great as the more alkaline one, due to the fact that at the concentra-

tion of calcium hydroxide giving a pH of 8.0 there is too little calcium present to support as rapid a growth as in the concentration having a pH of 10.0.

In addition to measurements of the rate of elongation of root hairs over a three-hour period beginning 13 hours after immersion, other measurements and observations were made upon the root and the root hairs at the time of immersion

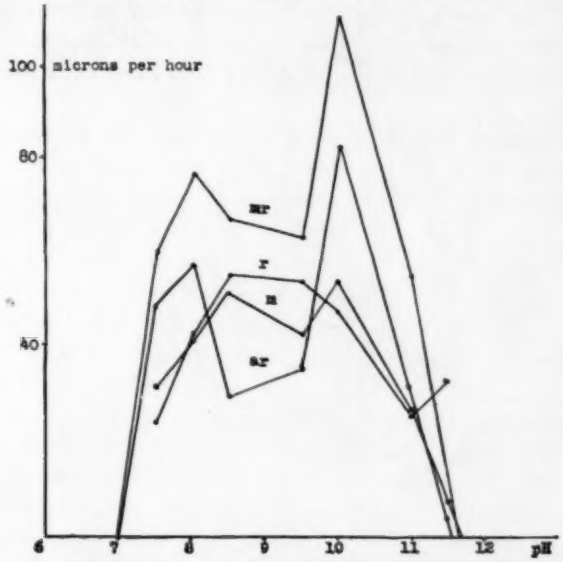

Fig. 18. Root and root hair elongation in calcium hydroxide.
mr: maximum rate of root hair elongation.
r: root elongation.
m: maximum length of root hairs after 12 hours.
ar: average rate of root hair elongation.

and 12 hours thereafter. These data are of interest here in attempting to discover whether the behavior of the root and of the root hairs in other respects is correlated in any way with the response of root hairs to different hydrogen-ion concentrations of this simple solution. Table 22 presents data regarding the elongation of three roots in each of the solutions studied, and the maximum length attained by aquatic root hairs in each case during 12 hours immersion

Figure 18 represents these data together with graphs for root hair elongation. It will be noted that the graph for maxi-

mum length of root hairs is almost identical with that for root hair elongation. We thus find that root hair elongation gives us the same type of graph with variations in pH whether the criterion be length of the longest hair after 12 hours immersion, or the most rapidly growing hair in each solution, or the average of a number of hairs as to growth rate.

The rate of root elongation, however, does not correspond to that of root hair elongation, except at low concentrations—that is, near neutrality. The curve for root elongation rises to a maximum at pH 8.5, and above this falls with increasing alkalinity.

In explaining this difference in the reaction of the root to the solution, it is to be noted that the amount of calcium hydroxide present in these solutions is exceedingly small. For changing the pH of two liters of distilled water to pH 7.5, 8.0, 8.5, 9.5, 10.0, and 11.0, the amounts of saturated solution of calcium hydroxide which were added were 2, 2.5, 3, 3.5, 4, and 9.5 cc., respectively. Consequently the molar solutions of calcium oxide employed were, respectively: 1.00^{-7}, 1.25^{-7}, 1.50^{-7}, 1.75^{-7}, 2.00^{-7}, 4.75^{-7}. It is apparent that from so very dilute a solution, the cells on the interior of the region of cell division and cell elongation will receive very little, if any, calcium from the ambient medium. The calcium will obviously be largely taken up at the surface, especially in the formation of calcium pectate of the root hair walls. We should therefore expect different results for the elongation of the root and the root hairs, respectively, in calcium hydroxide. The fact that the root is retarded with increasing alkalinity above pH 8.5 is evidence, however, that the OH ions do penetrate into the region of the cell elongation of the root. It seems likely that at the surface of the root hair the calcium of the calcium hydroxide is combined with pectate of oxalate anions, which come from a soluble organic salt, such as one of potassium. The hydroxyl ions are thus accompanied into the interior of the root by this potassium or similar ion. The latter, not being utilized in cell wall formation, has no stimulating effect upon elongation of the root, such as the calcium has upon the elongation of root hairs. Thus with increasing concentration of calcium hydroxide the root hair increases its growth rate up to pH 10.0, above which it grows more slowly, due to the over-

dose of OH ions. This retardative effect is apparent in the root at a much lower concentration, pH 8.5, since the calcium does not penetrate to stimulate growth and overcome the effect of the hydroxyl ions.

From the standpoint of the root hairs, then, a solution of pH 8.5 is decidedly hypotonic, as stated above. It is also apparent that the hydroxyl ions in these very dilute concentrations are sufficient to stimulate the elongation of the root above that obtaining in distilled water. Further addition of the base, however, making the pH greater than 8.5, results in an overdose of hydroxyl ions and hence retardation of root elongation. These higher solutions, however, do not retard root hair elongation, because they also bring additional calcium ions to these structures; and it is likely that their rate of elongation is determined in large measure by the amount of calcium available. Nevertheless, when the pH passes 10.0, the concentration of hydroxyl ions is so great as to overcome any stimulating effects of additional calcium, and the curve drops suddenly. This interpretation of the difference between root and root hair elongation is in harmony with the conclusions of Hansteen Cranner (9, 193) that the influence of external factors in toxicity occurs independently of the calcium on the interior of the root; but that the cause of toxicity is a surface effect. He finds that a root rich in calcium internally succumbs to injury on the surface by salts which calcium normally antagonizes. Only if the calcium is in the ambient medium is injury inhibited.

Various other features of root development, aside from rate of elongation of root hairs, elongation of roots, and maximum length of root hairs after 12 hours immersion in the solution are given in table 23 in detail, and the results are summarized in table 24. These features include: length of respective regions of the root; spacing of root hairs; distribution of root hairs on the affluent and effluent sides of the root; curvature of the root.

From the data given in these tables it will be observed that in calcium hydroxide solutions, unlike many of the solutions of calcium chloride previously reported upon (V), there is, except in pH 7.5, an entire absence of an interzone—that is, a hairless region between the zone of amphibious root hairs produced in the hair before immersion, and the zone of aquatic root hairs

TABLE 23

Root development in $Ca(OH)_2$

pH	ROOT NO.	TIP			s		i		SP	DIST	CURVATURE	
		o	*i*	*d*	*t*	*f*	*t*	*f*			*o*	*l*
7.5	1	1.5	1.5	0	1.5	1.5	0	0	10	::	*s*	*s*
	2	2.0	1.5	−0.5	3.0	3.0	0	0	20	::	*t*	*t*
	3	3.0	1.5	−1.5	1.5	1.5	0.7	0.7	20	::	*f*	*s*
8.0	1	1.5	1.5	0	1.5	1.5	0	0	30	::	*f*	*t*
	2	2.0	0.7	−1.3	1.5	1.5	0	0	30	::	*f*	*s*
	3	1.5	0.5	0	3.0	3.0	0	0	100	::	*f*	*s*
8.5	1	1.5	3.0	+1.5	4.5	4.5	0	0	50	::	*s*	*s*
	2	2.0	1.5	−0.5	7.5	7.5	0	0	40	*ft*	*s*	*f*
	3	1.5	1.5	0	7.5	7.5	0	0	40	*ft*	*s*	*s*
9.5	1	1.5	3.0	+1.5	4.5	4.5	0	0	50	::	*t*	*t*
	2	2.0	2.0	0	4.5	4.5	0	0	70	::	*t*	*t*
	3	2.0	3.0	+1.0	3.0	3.0	0	0	50	*ft*	*f*	*s*
10.0	1	1.5	1.5	0	6.0	6.0	0	0	70	::	*t*	*s*
	2	1.5	3.0	+1.5	3.0	3.0	0	0	60	::	*f*	*s*
	3	1.5	1.5	0	6.0	6.0	0	0	60	::	*s*	*f*
11.0	1	1.5	3.0	+1.5	0.8	0.8	0	0	20	::	*f*	*s*
	2	2.0	1.5	−0.5	1.5	1.5	0	0	70	::	*f*	*s*
	3	3.0	1.5	−1.5	3.0	3.0	0	0	30	::	*f*	*f*
11.5	1	3.0	3.0	0	1.5	1.5	0	0	200	*f*	*t*	*t*
	2	2.0	4.5	+2.5	0	0	0	0	—	—	*s*	*s*
	3	2.0	6.0	+4.0	0	0	0	0	—	—	*t*	*t*

TABLE 24

Summary and averages of root development in $Ca(OH)_2$

pH	TIP			s		i		SP	DISTRIBUTION					CURVATURE					
	o	*i*	*d*	*t*	*f*	*t*	*f*		::	*ft*	*f*	*tf*	*t*	*o*			*l*		
														s	*t*	*f*	*s*	*t*	*f*
7.5	2.2	1.5	−0.7	2.0	2.0	0.2	0.2	17	3					1	1	1	2	1	
8.0	1.7	1.2	−0.5	2.0	2.0	0	0	53	3							3	2	1	
8.5	1.7	2.0	+0.3	6.5	6.5	0	0	43	1	2				3			2		1
9.5	1.8	2.6	+0.8	4.0	4.0	0	0	57	2	1					2	1	1	2	
10.0	1.5	2.0	+0.5	5.0	5.0	0	0	63	3					1	1	1	2		1
11.0	2.2	2.0	−0.2	1.8	1.8	0	0	47	3							3	2		1
11.5	2.3	4.5	+2.2	0.5	0.5	0	0	—					1	1	2		1	2	

The symbols employed in these tables are to be interpreted as follows:

tip: length of hairless portion of root tip in mm.

s: length of zone of aquatic root hairs in mm.

i: length of the interzone, that is the region between the zone of aquatic root hairs and the zone of amphibious root hairs, in mm.

sp: approximate average spacing or distance between adjacent root hairs on the horizon on the root in microns.

dist: distribution of root hairs,

:: : about equal number on affluent and effluent sides.

ft: more root hairs on effluent than on affluent side.

f: root hairs only present on effluent side.

In the two columns under *curvature*, the first indicates the original direction (*o*), and the second the final direction (*l*), indicated by the letters: *s*, straight, *t*, toward the current; *f*, in the direction with the current.

produced after immersion. It seems clear that the interzone results from rapid root elongation accompanied by a temporary suppression of root hair development. It is reasonable to expect, then, that in pH 7.5, where root elongation as well as root hair elongation (figure 18) are accelereted as compared with pH 7.0, there will be some roots which will develop an interzone. This occurred in our experiment in one of the three roots observed. In more alkaline solutions of calcium hydroxide, however, we find that root elongation is more and more suppressed, while root hair elongation rises to a maximum at pH 10.0. It would not be so reasonable, then, to expect the occurrence of interzones in these solutions; and these tables show that none are found here. The occurrence and absence of the interzone in these solutions thus constitutes further evidence that the concentration of calcium is not sufficient to accelerate root growth; but that its effect is entirely superficial—namely, upon the root hairs alone. It seems, however, that the hydroxyl ions do penetrate into the growing region of the root.

This conclusion is also supported by the tendency of the root to assume a vertical position. While only 6 of the 21 roots were straight at the time of immersion, 12 of them were straight 12 hours later. Those that were turned toward the current originally, with one exception, remained that way; while all, except 3, of the 9 that were turned from the current became vertical, or, in one case, turned toward the current. The data, therefore, indicate that the difference in the concentrations of the ions on the two sides of the root is not sufficient to overcome the effect of geotropism. This is obviously due, not to an absence of a difference, but to the failure of the solution, in whole or in part, to penetrate into the growing region of the root.

This tendency of the roots to straighten in these solutions is also apparently correlated with the equality of the number of root hairs on the two sides of the root. It is to be noted that of the 18 roots which produced root hairs, only three did not have them equally distributed on the two sides of the root. These exceptions had more hairs on the effluent than on the affluent side. It is also to be noted that the length of the zone of aquatic root hairs was the same on the two sides. It was, however, shown above (table 21) that the rate of root hair elongation is not the same on the two sides of the root. In

low concentrations it was greater on the affluent side, and in higher concentrations on the effluent side. It thus appears that the rate of root hair elongation is a far more sensitive index of the effect of the solution upon protoplasmic activity, than any other feature of root development.

Two series of data (table 23)—namely, the length of the zone of aquatic root hairs and the spacing of the root hairs—give, when plotted, pH curves which correspond closely to those (figure 18) for maximum rate of elongation of root hairs, average rate, and maximum length. In all five of these curves, one optimum is at pH 10, and the other at pH 8.0 or 8.5, with a median minimum at 8.5 or 9.5. It is to be noted, however, that the greater optimum for the length of the zone of root hairs is the one with the higher hydrogen-ion concentration, rather than the more alkaline one, as is the case in the other four graphs. This is evidently the result of the drop in the curve for root elongation with increased alkalinity above pH 8.5 (figure 18). It thus would seem that the length of the zone of root hairs is a resultant of factors determining root hair elongation, and also root elongation. It is, therefore, not as simple a criterion of reaction to the medium, as are the other factors studied.

One other series of data shows a correspondence to the graph for root elongation. This is increase in length of the hairless tip during the 12 hour period. Inasmuch as the hairless tip contains the region of cell elongation it is not surprising to find that, in solutions supporting more rapid root elongation, this growing region itself is longer. However, it must be borne in mind that in the root the region of cell elongation, or the entire region of growth for that matter, does not necessarily itself become longer. The region of growth contributes to the region of absorption, which in turn contributes to the length of the region of storage and conduction. It is thus the proximal rather than the distal part of the root which actually becomes longer in growth. It does not necessarily follow, therefore, that because a root grows faster in one solution than in another the region of growth will be longer. Nevertheless the data presented above indicate that such is the case in this instance.

As a result of this analysis of root development in its various aspects, which can be mathematically determined, it seems that root hair elongation and root elongation are the

most precise and dependable series of data which can be obtained as evidence of the response of the plant to its ambient medium. Other aspects of root and root hair development give results which correspond to one or the other of these two, or give graphs which are intermediate. Their results are, however, not as consistent nor as accurately determinable as is rate or amount of root and root hair elongation.

The effect of the solution upon root and root hair elongation respectively is, however, not entirely different. In fact, it has been previously shown that in single calcium salt solutions of optimum or higher concentration, these two criteria give almost identical results. It is in the more alkaline solutions of calcium hydroxide that the most striking disparity occurs. This has been interpreted above as due to a difference in the depth within the root to which the calcium and the hydroxyl ions of the solution penetrate, respectively.

In this and in the previous papers of the series the interpretation of the effect of the solution upon root and root hair development has been based upon the hypothesis that the mechanism concerned is cell wall formation. It has been suggested that, inasmuch as the outer layer of the root hair and the middle lamella of the partition walls of the root are composed very largely of calcium pectate, a calcium solution affects the rate of cell wall extension by controlling the amount of calcium available for that wall formation. In this connection it is interesting to note that Tschirch (198) regards the secondary lamellae also as consisting of a calcium cellulose compound. The control of the amount of available calcium is assumed to be accomplished in two ways, by the absolute amount of calcium present in the surrounding solution, and by the anion present. The latter is regarded as affecting the permeability of the cell membrane to calcium. It thus seems that the calcium must enter the interior of the root hair and there react with some such compound as potassium pectate, forming an insoluble calcium pectate which is deposited in the wall at the growing tip of the hair, or that, if potassium pectate is not present, it may be transferred to the root interior, where it will undergo similar deposition in the middle lamella, or possibly the secondary lamellae of the partition walls. Loo (195) has recently studied the reaction of the nutrient solution during

plant growth. He considers that the chief function of calcium is to maintain the physiological balance of the nutrient solution. It has been shown above, however, that calcium does have a very direct relation to cell metabolism as related to cell wall formation and cell enlargement. Cerighelli (191) has recently studied the effects upon root length of cuttings of *Tradescantia*, *Tropaeolum* and *Mentha* of the addition of calcium sulphate or calcium carbonate to water doubly distilled in quartz. He finds that, whereas the roots became only 3 or 4 mm. long during 16 days in pure water, they attained a length during the same time of 40 to 90 mm. in the simple calcium salt solutions. His work, therefore, confirms our findings as to the direct effect of calcium upon root activity.

Heilbrunn (194) has recently shown that calcium must be present in order that the plasma membrane be regenerated after rupture, or, as he puts it, in order that a surface precipitation membrane be formed. He finds that it is not necessary that the internal calcium be removed; but only that there be an entire absence of calcium in the surrounding medium, in order that membrane formation be inhibited. His interpretation is in harmony with the conclusions of Hansteen Cranner (9, 193) referred to above. It also suggests that the effect of calcium upon root hair elongation may be not entirely a matter of cell wall formation, but of formation of the protoplasmic membrane as well.

In conclusion the author is very glad to gratefully acknowledge that the research reported in this paper was supported by a grant from the Fellowship Fund of the Society of Sigma Xi.

SUMMARY VII

65. A reinvestigation of the effects of calcium hydroxide upon the rate of root hair elongation confirms the results previously obtained, and furnishes a considerable amount of collateral evidence as to the nature of root and root hair growth.

66. The results indicate that in the very dilute solutions of calcium hydroxide which support root growth, the calcium ions are entirely consumed in root hair formation, and the hydroxyl ions penetrate and effect the rate of root elongation.

67. It is found that the length of the hairless tip gives results like that of root elongation; the spacing of the root hairs

results like those of root hair elongation; and the length of the zone of aquatic root hairs and the length of the interzone give results which are intermediate between those of root hair and root elongation. It is concluded that rates of root and root hair elongation, respectively, are the best criteria of the effect of the solution upon the root development.

68. Root elongation increases to a maximum at pH 8.5 and then falls off with increased alkalinity. Root hair elongation forms a bimodal curve with the greater optima at pH 10.0.

69. In calcium hydroxide there is a tendency for the roots to straighten, for the root hairs to be equally distributed between the side toward the current (affluent) and the side away from the current (effluent), and for the zone of aquatic root hairs to be the same on the two sides of the root.

70. The root hairs are, however, found to elongate more rapidly on the affluent side in nearly neutral solutions, and on the effluent side in more alkaline solutions, indicating that the rate of root hair elongation is a very sensitive response to the composition and hydrogen-ion concentration of the ambient medium. The difference in the behavior of the two sides is attributed to the absorption of calcium by the affluent side and the liberation of carbon dioxide by the affluent side, altering the concentration of these substances on the effluent side.

71. It is demonstrated that in a hypotonic solution the effluent side will be the poorest place for root hair development, and in hypertonic solutions the best place; whereas in all solutions the affluent side will be intermediate. The latter therefore gives the more precise measurement of the effect of the solution.

72. The almost entire absence of an interzone in roots in calcium hydroxide solutions is interpreted as due to the less favorable conditions for root development as compared with root hair development.

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Quercus neo-Ashei

BENJAMIN FRANKLIN BUSH

It would appear from the accounts of *Quercus marilandica*, in the manuals of the trees of North America, and the manuals and floras of the Eastern United States, that this species ranges as far west as western Texas and western Oklahoma. As I understand *Q. marilandica*, it is a species of the wooded Carolinian Zone, and ranges from New York to Florida, west to eastern Oklahoma and eastern and southern Texas and keeps entirely within the forested region of the Carolinian Zone.

Mr. Ashe has called my attention to the Black Jack Oak of the treeless plains and plateaus of middle and western Texas, which has been named *Q. marilandica Ashei* by Sudworth, and this tree seems to me to be distinct enough to deserve specific rank, on account of its slender glabrate twigs, smaller, more glabrate leaves, smaller acorns, smaller, differently-shaped cups, which have thinner more glabrate scales, and an entirely different range.

The name *Ashei* being preoccupied by *X Quercus Ashei* Trelease (Proc. Am. Phil. Soc. **61**: 48. 1917), I propose for this very distinct plains species the name *Quercus neo-Ashei*, to commemorate the discoverer, Mr. W. W. Ashe, who has insisted for years that this oak is distinct from the Black Jack Oak

The following comparisons will show the distinctions between this new species and *Q. marilandica*.

COMPARISON OF SPECIES

Leaves small, thinner, glabrate or grayish-pubescent beneath, with conspicuous tufts of yellowish tomentum in the axils of the principal veins beneath; buds small, 3–5 mm. long, ovate-lanceolate, grayish-pubescent; cups 10–15 mm. wide, rounded or flattened at the base, with small grayish-brown or red-brown scales closely appressed in a thin edge, covering less than one-third of the acorns; acorns 15–18 mm. long, glabrous, or nearly so, sometimes faintly striated..... *Q. neo-Ashei*

Leaves usually large, thick, leathery, usually rusty-tomentose on the under surface, less conspicuously tufted with tomentum in the axils of the three primary veins beneath; buds large, 6–8 mm. long, ovoid, or oval, promi-

nently angled, covered with rusty-brown hairs; cups 10–20 mm. wide mostly turbinate or hemispheric, decidedly tapering at the base, the scales at the thick edge squarrose or loosely imbricate, cinnamon-red; acorns oblong, usually broader below than above, about 18 mm. long, light yellow-brown, often striate, the shell usually lined with dense fulvous tomentum, inclosed for one-third to nearly two-thirds their length in the cups..... *Q. marilandica*

Quercus neo-Ashei n. sp.—*Q. marilandica Ashei* Sudworth, Jour. Forestry **20:** 167. 1922. A small tree, 8 to 25 feet high, with a trunk 6 to 18 inches in diameter, with very rough, dark brown or blackish bark, which is broken up into numerous more or less square, thick plates, 1 to 1.5 inches long; branches short, stout, crooked, forming a very irregular, small head; twigs and winter buds much more slender than those of *Q. marilandica*, grayish-pubescent, the buds ovate lanceolate, 3–5 mm. long; leaves much smaller and thinner than those of *Q. marilandica*, 4–8 cm. long, 4–6 cm. wide, broadly-obovate, 3-lobed or occasionally 5-lobed, the juncture of the three principal veins usually much above the middle, glabrous or grayish-pubescent beneath with conspicuous tufts of grayish-brown tomentum in the axils of the principal veins beneath, in contradistinction to the usually rusty pubescence of the under surfaces of the leaves of *Q. marilandica*; fruit 12–16 mm. thick, solitary or in pairs, usually pedunculate; cups 10–15 mm. wide, 5–7 mm. high, rounded or flattened at the base, with small grayish-brown or red-brown scales closely appressed in a thin edge, and covering less than one-third of the acorns; acorns 15–18 mm. long, 10–14 mm. thick, glabrous or nearly so, sometimes faintly striated.

On the high treeless plateaus of the Sonoran Zone of middle Texas, on the edge of the plains and on the foothills of low mountains, where it is the only form of Black Jack Oak found throughout the plateau region of middle Texas, where it occurs along arroyos and coulees in company with various forms of *Quercus stellata*, with *Q. Mohriana*, *Q. Laceyi*, *Q. virginiana*, *Q. annulata*, *Cercis Texana*, *Celtis Lindheimeri*, *C. reticulata*, *Juniperus monosperma*, *Carya Buckleyi* and *C. arkansana*, northward to middle and western Oklahoma.

SPECIMENS EXAMINED:

TEXAS: Smithwick, near Marble Falls, Burnet County, *Ashe 1012*, Sept. 6, 1921, (US) TYPE of *Q. marilandica Ashei*; cotype in (A)[1]; *Ashe*, in

[1] In the citation of specimens herbaria are designated as follows: Ashe herbarium (A); Arnold Arboretum (AA); United States National Herbarium (US).

1926 (A); Austin, Travis County, *Hall 603* (US, no. 39660); Crab Apple, Gillespie County, *Jermy 102*, two flowering shoots and one shoot with mature leaves, but no doubt both this species (US, no. 39667); Jack County, *Ashe 17* (A); McNeil, Travis County, *Ashe*, in 1921 (A); Jack County, *Ashe*, in 1921 (A); no locality given, Mexican Boundary Survey, *Parry 1376* (US, no. 39684); Brownwood, Brown County, *Palmer 29546* (AA); San Saba, San Saba County, *Palmer 11820* (AA).—OKLAHOMA: No locality given, *Palmer 257*, a flowering shoot (US, no. 39666); Comanche County, *Ashe*, in 1914, on the low mountains known as Wichita Mountains, where it is fairly common in places (A); Mount Scott, Caddo County, *Gant 164* (US, no. 609159).

QUERCUS MARILANDICA Muench, Hausv. **5**: 253. 1770. A tree 25–50 feet high, with a trunk 18–20 inches in diameter, occasionally more than this, covered with thick, rough, dark brown or nearly black bark, which is much broken up into nearly square plates 1–3 inches long; branches short, stout, contracted, spreading, forming a narrow compact or sometimes an open head; branchlets and twigs usually thick, angled, light brown, tomentose or scurfy-pubescent during the summer, reddish-brown and glabrate or puberulous in the winter, and ultimately brown or ashy-gray; winter buds about 6–8 mm. long, ovoid or oval, prominently angled, light red-brown, covered with rusty-brown hairs; leaves usually thick, leathery, broadly obovate and 3-lobed, or occasionally 5-lobed, the wide top end narrowing abruptly to a rounded or heart-shaped base, 12–17 cm. long and 8–12 cm. wide, the juncture of the three principal veins usually much below the middle of the leaf, the upper surface usually deep yellow-green and very glossy, in strong contrast with the rusty-pubescent under surface; fruit 14–22 mm. thick, solitary or in pairs, usually pedunculate; cups 15–20 mm. wide, mostly turbinate or hemispheric, decidedly tapering at the base, the scales at the thick edges are broad, truncate at the tips, squarrose or loosely imbricate, and cinnamon-red in color; acorns oblong, full and rounded at the ends, rather broader below than above the middle, about 18 mm. long, light yellow-brown and often striate, the shell lined with dense fulvous tomentum, inclosed for one-third to two-thirds of their length in thick light brown turbinate cups, puberulous on the inner surface, and covered by large reddish-brown, loosely imbricated scales, often ciliate and coated with loose pale or rusty tomentum, the upper scales smaller, erect, inserted on top of the cups in several rows, and forming thick rims round their inner surfaces, or occasionally reflexed and covering the upper half of the inner surface of the cups.

In dry, thin, sandy soil usually on high barren or rocky hills and ridges, or on borders of high, dry prairies, although often in low sandy bottoms in southern Illinois, southeastern Missouri

and eastern Arkansas, and occasionally in swamps and shallow water.

Long Island and Staten Island to Florida, northern Louisiana, eastern, southern and central Texas, Indiana, Kentucky, Iowa, Minnesota, Kansas, eastern Oklahoma, and eastern Nebraska, occupying therefore the forested region typical of the Carolinian Zone, associated with such species as *Quercus velutina*, *Q. stellata*, *Q. imbricaria*, and *Carya alba*.

SPECIMENS EXAMINED:

TEXAS: Jacksonville, Cherokee County, *Palmer 7139* (AA); Larissa, Cherokee County, *Bush 5603* (AA); Livingston, Polk County, *Palmer 6186* (AA); Inez, Victoria County, *Palmer 9141* (AA); Vanderbilt, Jackson County, *Palmer 9729* (AA); Riverside, Walker County, *Palmer 13176* (AA); Elgin, Bastrop County, *Fisher 99* (AA); Fort Worth, Tarrant County, *Palmer 14220* (AA); Edwards County, *Thorp 3362* (AA); Sutherland Springs, Wilson County, *Palmer 9210* (AA); Baird, Callahan County, *Palmer 13804* (AA); Utopia, Uvalde County, *Palmer 12941* (AA); Boerne, Kendall County, *Palmer 12909* (AA); San Antonio, Bexar County, *Schulz 725*.—OKLAHOMA: Poteau, Le Flore County, *Palmer 8282* (AA); Page, Le Flore County, *Palmer 20931* (AA); Mountain Park, Kiowa County, *Stevens 1274* (AA); Snyder, Kiowa County, *Palmer 13584* (AA); Sapulpa, Creek County, *Bush 694* (AA); Seiling, Dewey County, *Andrews 63* (AA); Hugo, Choctaw County, *Palmer 22490* (AA); Pawhuska, Osage County, *Stevens 1947* (AA); Oklahoma City, Oklahoma County, *Palmer 14618* (AA); No locality given, *Sheldon 305* (AA); Devil's Promenade, Ottawa County, *Bush 9646* (AA).—KANSAS: Arkansas City, Cowley County, *Palmer 21247* (AA); Neodesha, Wilson County, *Palmer 21145* (AA); Manhattan, Riley County, *Norton*, in 1894 (AA); Riley County, *Hitchcock*, in 1895. The sheet of Norton's collection has two shoots on it, one being good *Q. marilandica*, the other I take to be *Q. marilandica*×*velutina*. The last-mentioned collection, the one by Hitchcock, is also *Q. marilandica*× *velutina*. In the original description of *Q. marilandica Ashei*, Mr. Sudworth extended the range of this variety as far north as Riley County, Kansas, but I have seen nothing from Kansas that resembles *Q. neo-Ashei*, and it is very improbable that this species gets up to Riley County, Kansas, as it is a species of the plains country, and Riley County, Kansas, is a prairie region, and altogether different in formation from the plateau region of Texas.

COURTNEY, MISSOURI

A comparison of the available moisture in sod and open soil by the soil-point method

HENRY I. BALDWIN

INTRODUCTION

The porous porcelain soil-point (Livingston and Koketsu, 4) is, in its action, like an 'artificial root.' It absorbs water (soil solution) from the soil in which it is placed, and the initial rate of absorption is taken, for soils that are not very wet, as a measure of the capacity of the soil, at the given depth and location, to supply water to an absorbing surface such as that of a root. The soil-point method deals with the water-supplying power of the soil, not at all with the amount of water contained in the soil. Consequently, results secured by this method do not indicate the amount of available water present in the soil, but they indicate, instead, the initial rate at which the soil tested may supply water to plant roots. This dynamic characteristic of soil is of course the one by which the soil acts to influence the rate of absorption by root systems. Roots may absorb water from the given soil at any rate lower than the one indicated by the test, but never at a higher rate. When water-supplying powers are low enough they are limiting conditions for plant absorption, growth, etc.

While this method is probably susceptible of improvement in details, as is noted by its original authors (Livingston and Koketsu, 4) and by later workers who have employed it (Thone, 9; Mason, 7; Hardy, 2; Livingston, Hemmi, and Wilson, 3; Livingston and Ohga, 5; Wilson, 12), it remains the only method that is available for securing quantitative values of the water-supplying power of the soil. The small, porous-porcelain cones, each having an absorbing area of about 12 sq. cm. are placed dry in the soil at the points to be studied, and the readings are the amounts of water absorbed in a standard time period. These amounts are determined by weighing. The period of exposure has been 2 hours (Livingston and Koketsu, 1; Livingston, Hemmi, and Wilson, 3), or 1 hour (Livingston and

Ohga, 5; Wilson, 12) and it appears that the shorter period is more satisfactory and will become standard. Readings may be expressed, for comparison, in terms of rates per soil-point, or they may be expressed as milligrams of water that may be supplied across a single square centimeter of soil-root surface. The latter indices are secured by dividing each reading by 12.

The dynamic concept of soil-moisture conditions offers a new and valuable line of approach in ecological studies of soil-plant relations, and the soil-point method seems to be worthy of attention in connection with such studies. The present paper reports a very limited series of soil-point determinations made in the town of Grafton, Oxford County, Maine, in the summers of 1926 and 1927. In connection with the reforestation of a large tract of abandoned pasture land, it became important to know whether the small trees of white spruce, *Picea glauca* (Moench) Voss, to be planted should be set directly in the sod and moss or in a pit where the sod had been scraped away. Since this species, particularly in the case of trees over two years old, is very sensitive to deep planting (Lyons, 6, page 1004; Toumey, 10, page 385), drought danger cannot be warded off by setting the roots deeply in order to reach moister soil layers; it is important that they be spread as near the surface as possible, consistent with proper moisture supply and protection against frost heaving. It seemed possible that plants set directly in the sod and moss cover would be protected from frost heaving, and that frost damage to the tops might be lessened by the shade of the grass. In some cases a sod cover might perhaps be more effective in protecting the soil from insolation and consequent desiccation in times of drought than in withdrawing soil mosture by absorption and transpiration. Natural seedlings of white spruce have been observed here to have their roots only in the moss and sod layer, rarely penetrating the mineral soil until after 10 to 15 years of growth. Also, the thick, dense mat of sod formed by many plants of abandoned pastures, especially mosses like *Polytrichum commune* L., may be injurious by excluding oxygen from the tree roots and by hindering the warming of the soil by solar radiation. Alteration of these conditions may favor the development of raw humus; Barth (1) lists several plants which he believes are active

formers of raw humus. The average of over 40 hydrogen-ion determinations on the planting site here studied, by means of the Morgan type of soil-testing set, failed to show any considerable change in acidity after the removal of the sod. Both sod and underlying earth had a pH-value of from 5.2 to 5.5, which is well within the desirable range for white spruce. Other conditions that may be influential are the shading of the young trees by the grass, the possibility of greater nitrogen and other nutrient content in the sod layer and the presence or absence of beneficial mycorrhiza at the different depths.

White spruce occurs naturally in the original forest of this region only on sandy bottomlands along streams and lakes, and never on the uplands or in the northern hardwoods-spruce type of forest except near the northern limit of this type in central Quebec and Ontario. It is therefore likely that its invasion of abandoned pastures in Maine is due not so much to better moisture conditions there as to the absence in the pastures of conditions to which this species is intolerant during youth. Everywhere it does best with abundant moisture.

EXPERIMENTATION

To determine the effect of the sod cover on the moisture conditions soil-points were applied in the undisturbed sod, of mixed grasses and mosses, and in an adjacent small area from which the sod had been removed the preceding year. The level of the soil surface of the shallow pit formed by scraping away the sod was about 6 cm. lower than the level of the sod surface when the grass was pressed down. In each case and for each test two instruments were set into the soil about 10 cm. apart, so as to give readings for the 5 cm. depth. The exposure period was 2 hours and the two corresponding readings were averaged in each case.

Observations were made for the undisturbed sod and for the sodless area in May, June, and September, 1926, and in September, 1927, as shown in table 1, which also shows pertinent weather data and the numerical results. The weather was clear at the time of every observation.

It is at once apparent from these results that the initial water-supplying power of the soil was greater for the places from which the sod had been removed, and that this difference

became more pronounced as the season advanced. As Shantz (8) has pointed out, there is apt to be a progressive dissiccation of the soil with the advance of the season in such a climate as is here in question. It is also to be noted that grass and moss were brown, and transpiration must have been very slight in the spring, while in the fall these plants were still transpiring actively.

The influence of recent rains is shown clearly; within 24 hours after a rain, despite several hours of bright sunshine, practically

TABLE I

Water-supplying power of soil with and without sod cover

DATE OF OBSERVATION	HOURS SINCE LAST RAIN	BEGINNING OF 2-HR. EXPOSURE PERIOD	GRAMS OF WATER ABSORBED IN 2-HR. PERIOD, FOR 5 CM. DEPTH, PER SOIL-POINT		RATIO A/B
			Undisturbed sod (A)	Sod removed (B)	
May 24, 1926	24	1:30 P.M.	3.567	3.660	1
June 3, 1926	24	1:45 P.M.	0.453	0.524	1
Sept. 11, 1926	48	2:00 P.M.	0.552	2.266	4
Sept. 15, 1927	72	2:00 P.M.	0.129	2.626	24
Sept. 21, 1927	48	2:50 P.M.	0.365	2.746	9

no difference was indicated by the soil-points between sod and sodless soil. With longer rainless periods the difference between sod and sodless soil became correspondingly more pronounced. Weaver (11) has found that several species of broad-leaved trees grew much better on open soil than in competition with grass vegetation. Livingston and Ohga (5) concluded that for lawn grasses in Baltimore a water-supplying-power index of 0.1 gram per soil point for a 1-hour exposure might be considered critical, and that the maintenance of this or lower values for four or five days was sure to result in wilting and marked drought injury. Assuming this to be equivalent to a rate of 0.2 gram for the 2-hour exposure period used in the present tests (which is surely too high an estimate), it will be noted that the data here reported show one instance of a rate of less than 0.2 gram for 2 hours, and it is quite probable that values even lower than this might have been recorded in the summer. It seems to be clear from the few results presented above that the water-supplying-power of the soil will be generally higher in drought

periods for trees planted in open pits formed by the removal of the sod than for trees planted directly in the sod. It seems advisable to remove the sod from an area about 30 cm. square when seedling trees are to be planted.

In preparation of this little paper the writer has had valuable advice from Professor Burton E. Livingston, of Johns Hopkins University, from whom were secured the standard soil-points that were used.

BERLIN, NEW HAMPSHIRE

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